The University of Chicago

THE MORPHOLOGY OF THE SKULL OF A YOUNG GALESAURUS PLANICEPS AND RELATED FORMS

A PART OF A DISSERTATION SUBMITTED TO THE FACULTY OF THE DIVISION OF THE PHYSICAL SCIENCES IN CANDIDACY FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF GEOLOGY AND PALEONTOLOGY

1937

By

HAROLD WILLIAM RIGNEY

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THE MORPHOLOGY OF THE SKULL OF A YOUNG GALESAURUS PLANICEPS AND RELATED FORMS

HAROLD W. RIGNEY

Walker Museum, The University of Chicago, Chicago, Illinois

EIGHT TEXT FIGURES AND SIX PLATES

AUTHOR'S ABSTRACT

This paper is based on evidence obtained from sectioned skull of Galesaurus planiceps, Owen. Width-length index of skull is 67.7; height-width index 47.6. Dental formula is: $\frac{I\ 3\ or\ 4,\ C\ 1,\ PC\ 7}{I\ ?,\ C\ 1,\ PC\ 9}$. Length of prevomer is 24.0 mm., that of skull 62.0 mm. Maxilla contains cavity which appears to be equivalent of sinus maxillaris of mammals. Ear structure shows large internal auditory meatus. There is no evidence that horizontal and posterior semicircular canals pass through bone. Fenestra ovalis is large. Parasphenoid, basisphenoid, and basioccipital are fused. Parasphenoid consists of short body and a medial anterior process. Sella turcica lacks floor, probably due to erosion. Detached bone may be sphenethmoid. Dentary contains two canals, probably vascular. Comparisons with related forms lead to following conclusions: 1) Specimen is of young animal. 2) Dental succession of postcanines, distichical replacement of postcanines, long prevomer, short parasphenoid, incomplete osseous incasement of semicircular canals, and other characteristics label Galesaurus as primitive cynodont. 3) Reduction of parasphenoid and development of prevomer support Broom's view that Ictidosaurus is not a cynodont. 4) Prevomer as nasal septum; fusion of parasphenoid, basisphenoid, and basioccipital; large lacrimal, splenial, and articular; and other characteristics indicate that Galesaurus is off line leading to mammals. 5) In certain respects cynodonts are more mammal-like than gorgonopsians.

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INTRODUCTION

The cynodont skull treated in this study was found by the South African Expedition of Walker Museum of The University of Chicago, on September 13, 1929, at Fairy Dale, 20 miles northeast of Bethule, Orange Free State, South Africa. It was found associated with Lystrosaurus, in the Lystrosaurus zone of the Karroo Beds. It was no. 132 of the expedition and no. 1563 of the collection of Walker Museum.

The skull, as received by the writer, was partly cleaned of the hard, green, limy siltstone matrix, as shown in plate 1, A and B. There was sufficient exposure of the specimen to show that most of the left side of the skull, the tip of the snout excepted, and the left ramus were well preserved. The occipital region appeared somewhat damaged. The left ramus was turned away from the median line, exposing the teeth, but the crown of the teeth had been ground away in the process of cleaning. A well-preserved upper right molar showed the outline of a Galesaurus planiceps postcanine.

On the bases of this tooth, the configuration of the bones of the dorsal side of the skull, and the general outline of the fossil, the specimen was determined to be Galesaurus planiceps. The left half of the skull was 62.0 mm. long and 21.0 mm. wide.

ABBREVIATIONS

a., angular
a.c., alveolar canal
ar., articular
bo., basioccipital
bs., basisphenoid
c., canine
ch., choana
d., dentary
e., epipterygoid
ec., ectopterygoid
eo., exoccipital
f., frontal
f.f., foramen faciale
f.i., foramen incisivum
f.j., foramen jugulare
f.m., foramen magnum
f.o., foramen ovale
f.p., foramen pineale
f.pal., foramen palatinum
f.pit., foramen pituitarium
f.pt., foramen posttemporale
f.s., foramen septomaxillare
f.v., foramen vasculare
fe.o., fenestra ovalis
fe.r., fenestra rotunda
j., jugal
i.c.1, first intercentum
l., lacrimal
l.c., lacrimonasal canal
m., maxilla
ml., molar
n., nasal
o., opisthotic
o.f., orbital fissure
p., prearticular
pa., parietal
pl., palatine
pm., premaxilla
po., postorbital
pr., prootic
pra., proatlas
prf., prefrontal
ps., parasphenoid
pt., pterygoid
pv., prevomer
sa., surangular
sm., septomaxilla
so., supraoccipital
sp., splenial
sph., sphenethmoid
sq., squamosal
s.t., sella turcica
t., tabular
u., unidentified

The specimen was sectioned by grinding and records were made at regular intervals. The first eleven sections or surfaces were 1.0 mm. apart; the remaining ones, from no. 12 to no. 112, 0.5 mm. Peel records of nitrocellulose were taken of all surfaces from nos. 1 to 36, and thereafter at multiples of

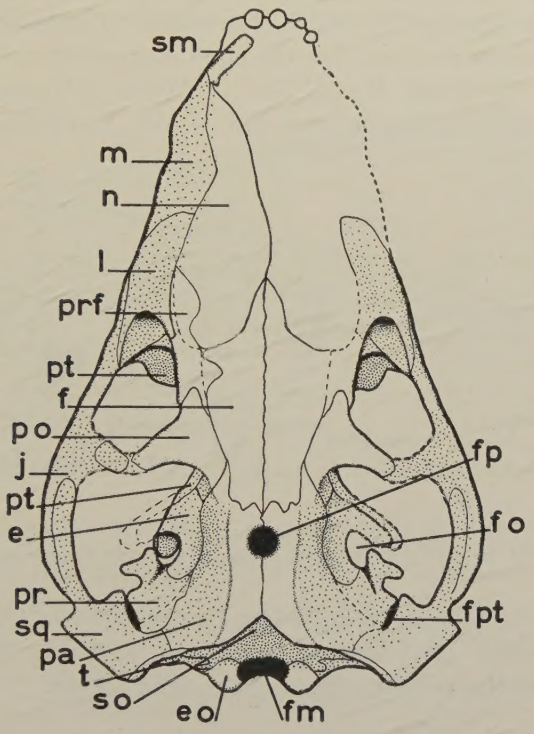

Fig. 1 Dorsal view of reconstructed skull of a young Galesaurus planiceps.

5 from surface no. 40 up to and including no. 80. All surfaces from no. 9 to no. 112 were photographed. The enlargement was usually $\times$ 2, in some cases it was more, but, with the exception of section 11, which is about $\times$ 2.25, never more than $\times$ 2.16.

A wax model of $\times$ 4 enlargement was made of beeswax plates, which portrayed, in three dimensions, the general configurations of the skull.

Figures 1 to 6, inclusive, were based on drawings made on graph paper from the photographs of the surfaces of no. 9 to no 112 and photographs of the peels of sections no. 3 to no. 8.

I am indebted to Dr. Everett Claire Olson of the Department of Geology and Palaeontology of The University of Chicago for placing the skull of Galesaurus planiceps at my disposal and am grateful for his encouragement and criticism. I also wish to thank Mr. Miller of Walker Museum for his help in the laboratory work. Dr. G. W. Bartelmez and Dr. Jeannette Obenchain, both of the Department of Anatomy of The University of Chicago, rendered valuable advice and assistance in the construction of the wax model.

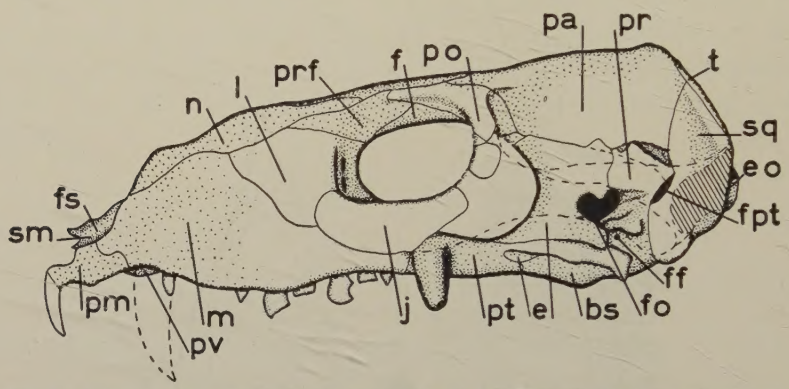

Fig. 2 Lateral view of reconstructed skull of a young Galesaurus planiceps.

DESCRIPTION OF SKULL AND JAW RECONSTRUCTED FROM SECTION RECORDS

The following descriptions of the skull and jaw in general, and of the separate bones are based on reconstructions made on graph paper of the various aspects of the skull. The peels and photographs of the sections were referred to constantly for details not shown on the drawings.

In general outline the skull is wide and low, being widest in the region of the zygomatic arches. It has a rather blunt snout. The length, measured on the median line from the

lowest edge of the premaxilla, between the median incisors, to the line drawn from the most posterior point of the condyles, is 62.0 mm. The width, measured between the widest points on the zygomatic arches, and 3.0 mm. posterior to the center of the parietal foramen, is 42.0 mm. The greatest height, measured at the protuberance formed by the union of the occipital crests, is 20.0 mm. The relative measurements

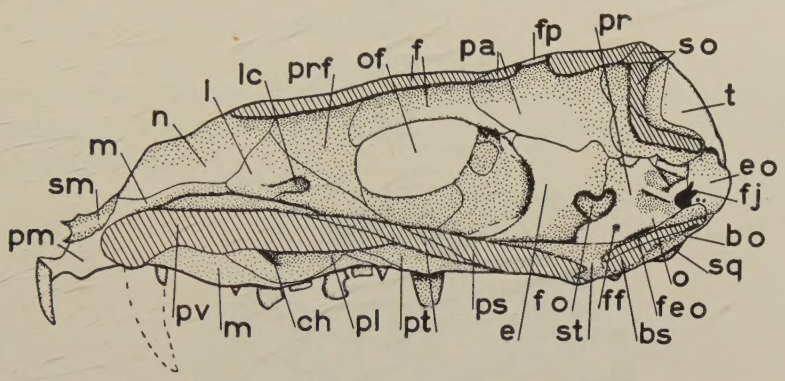

Fig. 3 Medial view of reconstructed skull of a young Galesaurus planiceps.

of the width to the height, and the height to the width of the skull may be expressed by the following indices:

$$\frac{\text{Width} \times 100}{\text{Length}} = \text{Width-length index} = 67.7$$

$$\frac{\text{Height} \times 100}{\text{Width}} = \text{Height-width index} = 47.6$$

Throughout the descriptions which follow, when dealing with paired elements, whether of cartilages, bones, nerves, or blood vessels, only the left member will be considered.

Maxilla. The maxilla forms a considerable portion of the lateral wall of the snout. It is composed of a corpus, frontal process, zygomatic process, palatal process, and alveolar process. The corpus, long and rather inconspicuous, incloses a cavity which appears to be the sinus maxillaris. This cavity opens into the nasal cavity dorsal to the secondary palate and anterior to the palatine. It extends anteriorly, narrowing as

it proceeds, to a point situated below the posterior elongation of the roots of the canine, where it seems to end blindly. This cavity also may have served as the cynodont equivalent to the mammalian canalis alveolaris, in which case the cynodont equivalents to the mammalian arteria alveolaris superior and nervus alveolaris superior entered, perhaps, through canals

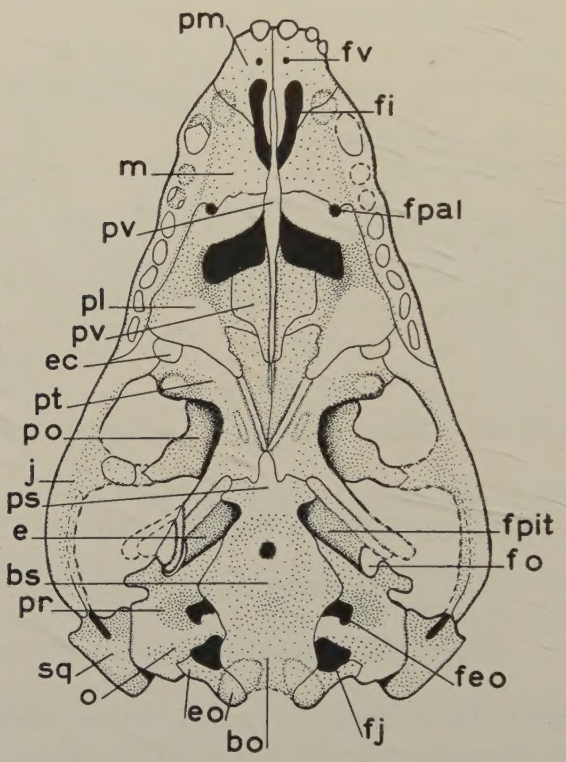

Fig. 4 Palatal view of reconstructed skull of a young Galesaurus planiceps.

in the lateral wall of the maxilla anterior to the jugal. This part of the lateral wall of the maxilla has been damaged, destroying the evidence of the presence or absence of such canals. F. R. Parrington ('34), however, reports two large foramina in the maxilla, above the fifth and sixth postcanines of Galesaurus planiceps.

Dentition. The upper teeth in this specimen are confined to the alveolar edges of the premaxilla and maxilla. There is no evidence of palatal teeth. The premaxilla, as preserved, bears one incisor on the right side and three on the left. There is room on the left side for only one more, setting the number of incisors probably at four.

The maxilla carries one damaged canine and six eroded postcanines, the second to the seventh. There is an empty socket for the first postcanine.

Most of the crown of the canine is missing, so that its outline is a matter of conjecture. The socket bows dorsoposteriorly, ending at a point dorsal to and between the first and second postcanines.

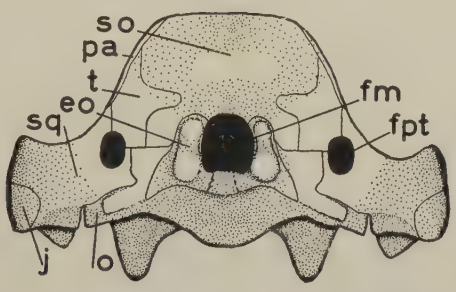

Fig. 5 Occipital view of reconstructed skull of a young Galesaurus planiceps.

The postcanines are elongated anteroposteriorly and are somewhat crowded.

In the lower jaw there is one incisor, the last one, preserved, one canine, and nine postcanines. Replacement of the eighth postcanine seems to be in progress. The postcanines, like those of the upper jaw, are elongated in the anteroposterior axis.

The dental formula is:

$$\frac{\text{I } 3 \text{ or } 4}{\text{I?}} \qquad \frac{\text{C } 1}{\text{C } 1} \qquad \frac{\text{PC } 7}{\text{PC } 9}$$

An upper right postcanine was preserved. Before grinding, this tooth was studied and found to have two cusps. The anterior cusp was the larger and recurved caudally over the

smaller posterior one. The latter cusp was slightly inclined craniad. This is a typical postcanine for Galesaurus planiceps.

Lacrimal. The lacrimal is a pentagonally-shaped bone proportionally larger than that in the average cynodont. Medial to the crista lacrimalis is a fossa. From this fossa lead two canals which are arranged, one above the other, in a dorsoventral line. These canals, leading anteriorly, meet to form the lacrimonasal canal which opens mediocranially into the nasal cavity.

Prevomer. The prevomer is well preserved. It consists of a long medial blade and a transverse process on either side. The medial blade may be divided into posterior and anterior parts. The posterior extra-nasal part extends, from its union

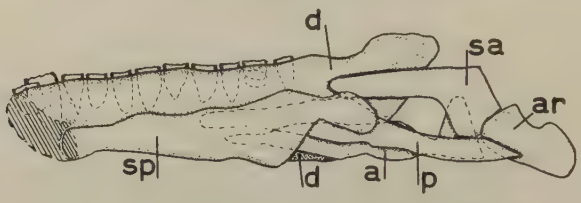

Fig. 6 Medial view of reconstructed jaw of a young Galesaurus planiceps.

with the pterygoid, anteriorly to the posterior edge of the secondary palate. From its dorsal borders, the transverse processes extend to either side, spreading ventrally to the palatines. The anterior part serves as a medial septum for the nasal cavity and a hanging support for the secondary palate which is formed from the palatal processes of the premaxilla, maxilla, and the anterior part of the palatine. Most of the dorsal edge of this part of the prevomer is a trough, probably for the reception of the nasal septum.

The maximum length of the prevomer is 24.0 mm. The maximum height, which includes the flanges of the dorsal trough, is 4.5 mm. The greatest width, which includes both of the transverse processes, is 7.0 mm.

Opisthotic. The opisthotic is a massive bone which forms the posterior bony structure of the inner and middle ear.

Anteriorly it is fused with the prootic. Some of the bone goes to form part of the posterior floor of the brain case, and an ascending lateral part contributes to the posterolateral wall of this structure. Much of this ascending part has been so damaged that its limits cannot be determined. Sections 7 and 8 show that the medial wall of the posttemporal canal, formed by the opisthotic, is not preserved.

From the medial view may be seen the subarcuate fossa, the bony casement for the inner ear, and the jugular canal complex.

The subarcuate fossa is located in the dorsal region on the ascending part of the opisthotic and perhaps the adjoining ascending part of the prootic. The posterior part of the subarcuate fossa is missing because of the erosion of the region

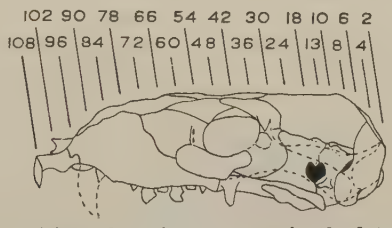

Fig. 7 Position of sections as seen in the lateral view.

of the caudal part of the ascending portion of the opisthotic. Ventral to this fossa is a medially extended ledge.

Ear region. The ear structure is damaged and eroded in the posterolateral region as is evident from sections 7, 8 and 9.

From the preserved part, however, the following structure may be determined. The internal auditory meatus is large. Three semicircular canals are present. The anterior semicircular canal passes through the ascending process of the prootic. There is no evidence that at any point the horizontal and posterior semicircular canals pass through bone. The fenestra ovalis is large and situated ventral to the horizontal semicircular canal. The diverticulum of the vestibule, containing the ampulla of the posterior semicircular canal, is probably shown in section 7. The cranial nerve VII passes

through the prootic, anterior to the vestibule of the ear. The caudal part of the posterior foramen of the facial canal is seen in section 15. Sections 16 and 17 show this canal passing anterolateral through the prootic to the region ventral to the crista prootica. Medioposteriorly to the vestibule is the jugular canal which lies between the opisthotic and the basioccipital, and provides an outlet from the brain cavity for the jugular vein and cranial nerves IX, X, XI and XII. Two small canals for contributing branches of the cranial nerve XII are seen in section 7. In the same section, in the dorsolateral part of the canal, may be seen an opening into the region of the vestibule.

Fig. 8 Position of sections as seen in the palatal view.

Parasphenoid. The parasphenoid, basisphenoid and basioccipital are fused into a basal bone which forms the posterior part of the basicranial axis.

The parasphenoid may be regarded as that part of the basal bone anterior to the plane passing through the most medial extensions of the foramina pituitaria. The parasphenoid is composed of a massive, broad, short corpus and an anterior medial process. The medial process comprises a horizontal element and a ventral keel. The horizontal element extends anteriorly from the dorsal part of the corpus as a narrow horizontal structure which tapers to a point. This horizontal element is seen from section 37 to 48, a distance of about 5.5 mm. Ventral from the posterior part of this horizontal element is a medial, keel-like supporting plate, extending anteriorly from the mediocranial part of the corpus. This medial plate is seen from section 37 to 41, a distance of about 2.0 mm.

The parasphenoid is about 12.0 mm. long. Its maximum width, immediately anterior to the foramina pituitaria is 7.5 mm.

Basisphenoid. The basisphenoid is the middle segment of the basal bone. It is a thick, rather flat bone, which broadens posteriorly. The sella turcica is located in the anterior, medial part of this bone. The medio-posterior floor of the sella turcica of this specimen is missing, either because of erosion or, of the presence of a medial canal. In figure 4 a single medial opening is shown in designation of this absence of bone. The bone comprising the floor of the sella turcica does not fuse with the posterior wall of the sella but extends caudally, as a plate-like process, under the posterior wall of the sella. This plate-like process reaches back to the region of section 18 for certain and perhaps to that of section 17.

Exoccipital. The exoccipital is a small bone forming the lateral wall of the foramen magnum, and perhaps the posterior part of the lateral wall of the cranium. Most, if not all, of the occipital condyle is formed by the exoccipital. It forms the posterior and medioposterior walls of the foramen jugulare. Two small canals pass through the cranial part of this bone, from the cranium or the anterior part of the foramen magnum to the foramen jugulare. These canals probably served as passages for contributing strands of nerve XII.

Squamosal. The squamosal is a massive bone which connects the temporal arch with the posterior part of the cranium. Extending transversely across the cranioventral surface of the corpus is the fossa which apparently formed the dorsal wall of the external auditory meatus. Caudomedial to the posterior union of the jugal with the corpus and apparently cutting across the floor of the fossa of the external auditory meatus is a long slit which may well have served as the groove for a process of the quadratojugal. The corpus forms the ventral half of the posterior rim of the posttemporal foramen and ventrolateral wall of the posttemporal canal. The anterior process lies dorsomedial to the posterior process of the jugal, while the medial process overlaps the tabular and forms

the lateral wall of the posttemporal canal and the lateral and dorsal rim of the anterior foramen of this canal.

Sphenethmoid (?). Sections 20 to 30, inclusive, show a trough-like bone with the mouth of the trough opening ventrolaterally. This is interpreted as being, most probably, the sphenethmoid, out of place and almost upside down. This seems to be a single or a fused pair of bones. The anterior part is divided, in what appears to be the medial plane. The convex side of the bone, which according to the writer's interpretation would be the ventral side of the bone in place, is grooved. Probably this groove held a medial septal bone or cartilage.

The sphenethmoid (?) is about 5.5 mm. long. Its maximum width is about 5.0 mm. Its greatest height is about 4.5 mm.

Dentary. The dentary of this specimen is fairly well preserved, so that all its structure, with the exception of the posterior part which has been eroded, can be worked out. The dentary is the largest element in the jaw.

There are two canals in the dentary of this specimen which probably served to carry blood vessels and nerves to the teeth. The posterior of these canals begins with its posterior foramen caudoventral to the last postcanine tooth. Caudal to this foramen is a groove which seems to have conducted vascular and nerve tissues to it. The posterior canal extends anterior from sections 63 to 72, a distance of about 4.5 mm. Craniad to this point it cannot be traced. The anterior canal begins with its posterior foramen in the ventral edge of the corpus between the fifth and sixth postcanines and extends anteriorly to the region of the tip of the dentary, a distance of about 12.0 or 13.0 mm. Anteriorly the canal seems to terminate with a foramen opening medially.

Angular. The angular consists of a long trough-like corpus and probably a thin plate-like posterior process projecting from the dorsal lateral part of the corpus. All evidence of an angular process has been lost. There was an angular process similar to that of Thrinaxodon putterilli (Broom, '32 b). This, however, was broken off and lost in the process of a remounting in plaster of Paris.

Coronoid, interparietal, quadrate, stapes and quadratojugal. These bones are missing in this skull.

DESCRIPTIVE NOTES ON THE SECTIONS

The following descriptive notes are not intended to be complete, but only to point out certain important features in selected sections.

Of the 112 sections made, only 41 are published. The published sections 4 to 15, inclusive, represent intervals of 1.0 mm.

TABLE 1

Dimensions of single bones

NAME OF BONE	LENGTH	WIDTH	HEIGHT
	mm.	*mm.*	*mm.*
Angular, incomplete	20.5+	1.5	4.5+
Articular	7.7	3.7	5.0
Basioccipital, incomplete	6.5	8.0+	
Basisphenoid, incomplete	8.5	10.0+	
Dentary, incomplete	35.0+		8.5+
Ectopterygoid	1.3	3.0	
Epipterygoid, incomplete	11.5		8.5
Exoccipital	4.5	5.5	6.0
Frontal, incomplete	19.5	6.0	
Jugal, incomplete	30.0		10.0
Lacrimal	13.0	4.0	8.0
Maxilla	26.0	9.0	12.0
Nasal, incomplete	22.0+	7.5+	
Opisthotic, incomplete		8.0	
Palatine	15.5	10.5	6.0
Parasphenoid	12.0	7.5	
Parietal, incomplete	18.5	8.5+	9.0+
Postorbital, incomplete	11.5+	7.5+	
Prearticular	26.5		4.0
Prefrontal	12.0	4.5	7.5
Premaxilla, incomplete	9.0+	5.0+	
Prevomer	24.0	7.0	4.5
Prootic, incomplete	7.5	7.5	11.5+
Pterygoid (quad. proc. incomplete)	21.5	10.0	
Septomaxilla	4.0	1.5	2.5
Sphenethmoid (?)	5.5	5.0	4.5
Splenial	26.0		6.0
Squamosal, incomplete	17.0	6.5	15.0
Supraoccipital, incomplete		18.0	11.0
Surangular, incomplete	15.0+		6.5+
Tabular	5.0	5.5	9.0

Sections 15 to 102, inclusive, are spaced 1.5 mm. apart except sections 21 to 24, inclusive, which are spaced at intervals of 0.5 mm. to show all the available evidence bearing on the sella turcica.

The sections are numbered beginning with the posterior end of the skull.

Unless stated otherwise, all notes refer to the elements of the left side of the skull.

Section 4. This section shows two parts of the exoccipital. The lower part is the occipital condyle. Two islands of bone lateroventral to the exoccipital are interpreted as belonging to the postcranial skeleton, the upper one being the proatlas and the lower one, the first intercentrum.

Section 5. Part of the foramen magnum is seen medial to the exoccipital.

Section 6. The posterior part of the foramen jugulare is sectioned showing a small canal leading from it to the foramen magnum, through the exoccipital. This small canal is interpreted as the posterior of two canals for strands of cranial nerve XII. The alternative interpretation would regard this opening as the posterior end of a flat, slit-like, but single foramen for cranial nerve XII. This latter interpretation seems improbable since most nerve canals are round in cross section; moreover, two canals in this region are characteristic of the cynodonts.

Section 7. This section is the first through the inner ear, exposing in the opisthotic the posterior semicircular canal and its ampulla. To all appearances a dorsolateral extension of the opisthotic which served as the lateral wall of the inner ear has been destroyed. Because of this destruction of the upper part of the opisthotic there is no preserved wall of bone between the posttemporal canal and the inner ear. The foramen jugulare is seen at approximately its greatest width. Two small canals are seen leading from the cranial cavity to the foramen jugulare. A laterodorsal opening from the foramen jugulare into the inner ear is apparent. This opening may have served as the fenestra rotunda of the mammals.

Section 8. The tabular seems to be fused with the parietal. The vestibule of the inner ear, from which leads the 'fenestra rotunda,' appears in the medial part of the opisthotic. The dorsolateral extension of the opisthotic is missing as in section 7. The internal auditory meatus is seen as a large opening.

Section 9. The opening in the supraoccipital seems to be the cranial cavity. The cranial tip of the tabular is sectioned. The anterior foramen of the posttemporal canal is seen dorsal to the junction of the squamosal and opisthotic. The horizontal, and perhaps the anterior semicircular canals, are seen in the opisthotic. The internal auditory meatus is larger than in section 8. Between the squamosal and the opisthotic is a wide opening interpreted as a groove for a process of the quadratojugal.

Section 10. The opening in the dorsal part of the supraoccipital is undoubtedly the cranial cavity. About 4.0 mm. of the ventrolateral edge of the parietal has been eroded away. The anterior foramen of the posttemporal canal is still present. The prootic-opisthotic is complete. The anterior semicircular canal is exposed passing through the dorsal part of the prootic-opisthotic. The horizontal semicircular canal is seen as a fossa in the prootic-opisthotic. The internal auditory meatus is large. The fossa in the prootic-opisthotic lateral to the fenestra ovalis most likely provided room for the stapes. The boundary between the prootic and opisthotic is difficult to determine because of fusion, hence the label 'prootic-opisthotic.' Two fragments of unidentified bone are located between the jugal and the medial process of the squamosal. These are too large to be interpreted as quadrate or quadratojugal, since they extend several sections anteriorly.

Section 11. The photograph from which this drawing was made was enlarged about $\times$ 2.25, which exceeds the enlargement of any of the other drawings. The parietal continues with its ventral edge eroded. The dorsolateral part of the prootic is eroded away exposing part of the anterior semicircular canal. The subarcuate fossa is seen in the dorsal part of the prootic. Ventral to the subarcuate fossa is a ledge.

The horizontal semicircular canal is also seen. The fenestra ovalis is large and is here seen leading into the inner ear ventral to the horizontal semicircular canal.

Section 13. In the prootic, the horizontal semicircular canal and perhaps the cranial wall of the anterior semicircular canal are seen.

Section 15. The crista prootica is seen, projecting laterally from the prootic. Ventral to the crista prootica is a fossa leading to the foramen ovale. A groove for cranial nerve VII is also seen on the medial side of the prootic. In sections 16 and 17 the canal for cranial nerve VII is exposed leading through the skull. The inner ear region is no longer present.

Section 18. The foramen ovale is exposed. The posterior extension of the floor of the sella turcica is seen as a thin bone ventral to the basisphenoid. The cranial tip of the crista prootica is seen. The caudal top of the quadrate process of the pterygoid is shown out of place having its ventral side turned medially. An unidentified bone appears in the cranial cavity.

Section 21. The foramen pineale is exposed. The posterior process of the epipterygoid is seen in two parts, the dorsal one being in place, the other broken off and shifted medially. This displaced part lies near the quadrate process of the pterygoid which also is shifted medially. Two cranial processes of a bone out of place are sectioned. This bone is interpreted as the sphenethmoid.

Section 22. This section cuts near the maximum width of the foramen pineale. The sphenethmoid (?) is seen as a trough-shaped bone partly overturned. The caudal part of the sella turcica is exposed. The middle part of the floor of the sella turcica is missing, due either to erosion or to the presence of a canal. This opening is treated later in the discussion of the basisphenoid.

Section 23. The opening of the floor of the sella turcica is larger than in section 22.

Section 24. The sphenethmoid (?) appears as a single bone or a fused pair of bones.

Section 27. The frontal is exposed, dovetailing the parietal. The boundary between the parasphenoid and the basisphenoid is difficult to determine because of fusion, hence the label 'basisphenoid-parasphenoid.' The articular is sectioned near its most massive part.

Section 30. An unidentified bone lies dorsal to the epipterygoid.

Section 33. The fragment labeled 'j (or po)' is interpreted as being, most probably, part of the jugal, although it may be part of the postorbital. The parietal is thinning out. A misplaced bone is seen in the right orbital fissure.

Section 42. The base of the skull is sectioned near its narrowest part.

Section 45. The roof of the skull is sectioned at its narrowest part.

Section 48. The pterygoid has expanded laterally and the anterior base of the transverse process of the pterygoid is seen.

Section 57. In this section, which is immediately anterior to the orbit, the cranium is seen with a flat dorsum and upright walls. The fossa leading to the lacrimal ducts is seen in the lacrimal. The seventh and last upper postcanine is sectioned.

Section 60. The cut through the lacrimal is anterior to the double posterior canals which fork from the lacrimonasal canal. The root of the septum between these canals is seen. Erosion has removed the lateral wall of this canal. The sixth upper postcanine is sectioned.

Section 63. The caudal part of the anterior foramen of the lacrimonasal canal is seen opening into the nasal cavity. The fifth upper postcanine is sectioned. The alveolar part of the dentary is seen bearing the socket for the ninth, and last lower postcanine. The canal, which seems to be vascular in nature, shows up in the dentary.

Section 66. The medial edge of the palatine seems to be fused to the prevomer. The caudal part of the fourth upper postcanine is cut.

Section 69. The anterior end of the cranial foramen of the lacrimonasal canal is shown. There is an opening bounded by the palatine and the prevomer leading from the mouth cavity into the nasal cavity. What seems to be the alveolar canal is cut near or through its medial foramen which leads into the canal from the nasal cavity. The lateral wall of the alveolar canal is eroded. The dorsal part of the prevomer is grooved, probably for the nasalseptal cartilage. The fourth upper postcanine is sectioned. The cranial edge of the eighth lower postcanine is cut. Below this tooth is seen the anterior tip of an uncut tooth which probably is the second eighth postcanine.

Section 72. The choana is seen. The third upper postcanine is cut as also is the seventh lower postcanine. The lateral wall of what seems to be the alveolar canal is missing.

Section 75. The third upper postcanine appears. The vascular canal in the dentary, seen in sections 63 and 72, cannot be traced in this section.

Section 78. The medial edge of the nasal has suffered some erosion. What seems to be the alveolar canal has all its walls preserved. A fragment of the second upper postcanine is cut. The sixth lower postcanine is sectioned.

Section 81. The lateral and medial walls of the socket of the upper canine are eroded, while the root of the tooth is crushed. The secondary palate seems to be distorted by being dipped ventrally. The empty socket for the first upper postcanine is cut. The fifth lower postcanine is also cut. The posterior foramen of what seems to be a vascular canal is exposed in the ventral part of the dentary. This canal may serve to carry blood vessels and nerves to the teeth of the anterior part of the dentary.

Section 84. Either the secondary palate is dipped ventrally out of place or the prevomer is raised. The posterior edge of the fourth lower postcanine is sectioned.

Section 87. The foramen incisivum is exposed. The fourth lower postcanine is cut through the mid-longitudinal section.

Section 90. The eroded crown of the canine shows. The third lower postcanine is exposed.

Section 93. A pit is seen in the palatal region of the maxilla, to receive the crown of the lower canine.

Section 96. The second lower postcanine is sectioned.

Section 99. The septomaxilla is exposed as a nearly closed tube. The foramen incisivum is near its anterior end. The first lower postcanine is seen. The dentary is relatively massive.

Section 102. The lower canine is sectioned. The sections anterior to this section show one left and three right incisors with room for three more incisors on the left and one on the right. In this section is seen the anterior foramen of the canal which appeared in section 81 and is interpreted as a vascular canal.

COMPARATIVE MORPHOLOGY AND DISCUSSION

It is the object of this chapter to compare the skull of Galesaurus planiceps, which the writer has sectioned, with related forms and to discuss briefly the problems and results which such comparative studies bring to light. Comparisons are made between the sectioned skull and other skulls of the same species as well as between Galesaurus planiceps and other forms, particularly the three cynodonts, Thrinaxodon liorhinus, Seeley; Lycaenognathus platyceps (Seeley), Broom; Gomphognathus mastacus (Seeley), Broom; and the two gorgonopsians, Cynarioides gracilis, Broom; and Cyonosaurus longiceps, Olson; and the monotreme Ornithorhynchus paradoxus.

Data concerning the specimens of Galesaurus planiceps, other than the one described in this paper, were gathered from the works of Broom ('32), Watson ('20), Haughton ('24), and Parrington ('34); concerning Thrinaxodon liorhinus from Watson ('20), Broom ('12), and Parrington ('33); concerning Gomphognathus mastacus and Lycaenognathus platyceps, from Broili and Schroeder ('35); concerning Cynarioides gracilis, from Broom ('30); concerning Cyonosaurus longiceps, from Olson ('37) and concerning Ornithorhynchus paradoxus, from Watson ('16).

To simplify these studies and discussions the skull is considered from various aspects.

The facial region

The number of bones in the facial region of Galesaurus planiceps agrees with that of the other cynodonts. The gorgonopsians Cynarioides gracilis and Cyonosaurus longiceps have a preparietal which Galesaurus planiceps lacks. Ornithorhynchus paradoxus lacks a postfrontal, prefrontal, postorbital, lacrimal, and the jugal is reduced or absent.

The snout of the sectioned Galesaurus planiceps is relatively larger than that of Owen's type. In this regard it is similar to Van Hoepen's type of 'Blochinodon detinens.' (Van Hoepen, '16; Haughton, '24), which Broom ('32 a, b) has shown to be a young Galesaurus planiceps. This large snout is evidence that the sectioned skull is from a young animal.

The broad and rounded snout of the sectioned skull and of Owen's type specimen is also relatively large for a cynodont, although not quite so large as that of Cynosuchoides whaitsi (Haughton), Broom (Broom, '32 b). When seen in dorsal aspect, it is approximately of the same proportion as the snout of gorgonopsian Cynarioides gracilis. The snout of Ornithorhynchus, highly specialized in shape, is longer and narrower than that of Galesaurus planiceps.

Dorsal view

The outstanding characteristics of the dorsal aspect are the shape and size of the nasal bone and the presence of the anterior process of the frontal.

The nasal is large and broadened at both ends. It is relatively larger than the nasal of Owen's type specimen, and proportionately about equal to that of Van Hoepen's 'Glochinodon detinens' (Van Hoepen, '16; Haughton, '24), or young Galesaurus planiceps. This is additional evidence that the sectioned specimen is a young animal.

The posterior expansion of the nasal is characteristic of the cynodonts and the marsupials. It is not consistently present in the gorgonopsians, being absent in Cyonosaurus longiceps but slightly developed in Cynarioides gracilis. The condition in the monotreme Ornithorhynchus is comparable to that in Cynarioides gracilis.

The anterior process of the frontal is present in most of the cynodonts, although absent in both Lycaenognathus platyceps and Thrinaxodon liorhinus. The anterior process is present in some gorgonopsians, as, for example, Cyonosaurus longiceps.

This process is better developed in Galesaurus planiceps than in any other form which shows it. Such a process is lacking in Ornithorhynchus. The very strong development of the process is a special characteristic of Galesaurus planiceps, indicating that it is off the line of evolution leading to the mammals.

The lateral view

In lateral view, three large bones are apparent, namely, the maxilla, lacrimal, and jugal. A noteworthy characteristic is the double nasal ducts.

A large maxilla is characteristic of both gorgonopsians and cynodonts. Ornithorhynchus has a relatively large maxilla, considering that its snout is shallow and narrow.

The lacrimal is relatively larger than that found in other cynodonts, the gorgonopsians, and the primitive mammals. This seems to be one of the specializations of Galesaurus planiceps, which indicates that it lies off the line leading to the mammals.

The jugal is relatively large as it is in all cynodonts and gorgonopsians. It is less massive posteriorly than in Gomphognathus mastacus.

The teeth are considered in the section dealing with the palatal view.

The posterior part of the lacrimonasal duct forks into a pair of nasal ducts. This condition is found in other cynodonts and in some gorgonopsians but is lacking in Ornithorhynchus.

Here is additional evidence that Galesaurus planiceps is off the direct line leading to the mammals.

Palatal view

The palatal view presents a number of interesting characteristics, namely, the number and size of the teeth, the foramen incisivum, the size of the premaxilla, the secondary palate, and the ectopterygoid.

Dentition. The dental formula is:

$$\frac{\text{I 3 or 4}}{\text{I?}} \qquad \frac{\text{C 1}}{\text{C 1}} \qquad \frac{\text{PC 7}}{\text{PC 9}}$$

The number of postcanines is less than that of the other described specimens of Galesaurus planiceps. It would seem that the number of these teeth depends on the length of the snout which in turn, depends on the age of the animal. In discussing the differences in the number of postcanines in the specimens known to him, Broom ('32 a, b) writes the following:

That the specimens agree closely except for the number of the postcanine teeth will be seen from the following measurements: Owen's type has 12 teeth, which measures 26.0 mm. Broom's specimen has 11 teeth, which measures 23.5 mm. Van Hoepen's type has 9 teeth, which measures 19.5 mm. Natal Museum specimen has 9 teeth, which measures 18.5 mm.

The number of postcanines of this sectioned specimen, seven in number, measure about 15.0 mm. This proportion of the number of postcanines to their aggregate length agrees with that of the specimens listed by Broom. Hence the small number of postcanines is further evidence that the specimen under consideration is that of a young individual.

The postcanines and canine are located near the outer rim of the maxilla to allow room for the lower teeth which lie within the upper set, when the jaws are closed, as is evidenced by the position of the pit for the crown of the lower canine. This relative position of the sets of teeth may be primitive, in which case it would add to the proof of the primitive character of the sectioned specimen. Such a relative position of

the sets of teeth also found in many cynodonts, as Thrinaxodon liorhinus and Lycaenognathus platyceps, is characteristic of the gorgonopsians. In Gomphognathus mastacus the two sets of postcanines seem to meet when the jaw is closed.

There is no trace of palatal teeth. The absence of these teeth seems to be common in the cynodonts and is a mammalian trend.

This specimen shows the germ of the eighth lower postcanine replacement tooth. Distichical replacement, moreover, of the postcanines is indicated by the greater length of the third and fifth, over the other upper postcanines. Replacement of the caudal postcanines and distichical replacement are primitive characteristics inherited from the earliest tetrapods and the primitive bony fishes (Parrington, '36).

The foramen incisivum is relatively larger in the specimen under consideration than in Thrinaxodon liorhinus, Gomphognathus mastacus, and Lycaenognathus platyceps. This large size is probably due to incomplete development of the secondary palate and hence would stand as a primitive characteristic.

The secondary palate does not extend as far posteriorly in Galesaurus planiceps as it does in Thrinaxodon liorhinus, Lycaenognathus platyceps, Gomphognathus mastacus, and Ornithorhynchus. This short secondary palate is a primitive characteristic.

The very presence of a secondary palate, common to the cynodonts, and its increase in length in the group are mammalian trends.

The premaxilla is relatively small as compared to that of the other cynodonts. It includes only the anterior part of the foramen incisivum and is too small to enter into more than the cranial wall of the pit for the crown of the lower canine. In Gomphognathus mastacus, the premaxilla includes most of this pit. The anterior half of this pit in Thrinaxodon liorhinus and Lycaenognathus platyceps is made of the premaxilla.

The ectopterygoid in the sectioned specimen is proportionately of a smaller size than the ectopterygoid of Thrinaxodon

liorhinus, Gomphognathus mastacus, and Lycaenognathus platyceps. It is relatively much smaller than that in Cyonosaurus longiceps and Cynarioides gracilis. The diminution of the ectopterygoid is a mammalian tendency.

The quadrate process of the pterygoid is equally well developed in both Galesaurus planiceps and Thrinaxodon liorhinus but absent in Gomphognathus mastacus and Lycaenognathus platyceps. This process is a primitive characteristic. It is found well developed in the gorgonopsians. In Cyonosaurus longiceps it is less developed than in Galesaurus planiceps and Thrinaxodon liorhinus, indicating that regarding this characteristic the gorgonopsian Cyonosaurus longiceps is more advanced than these two cynodonts.

Medial view

The medial view exposes a large prevomer, a small parasphenoid, and the opening of what seems to serve as an alveolar canal as well as a maxillary sinus.

The prevomer is the largest medial bone in the skull under discussion. It is about equal to the combined length of the parasphenoid, basisphenoid, and basioccipital bone. The prevomer of this form is relatively shorter than that in such cynodonts as Thrinaxodon liorhinus, Gomphognathus mastacus, and Lycaenognathus platyceps, and is relatively larger than that of the gorgonopsians, Cyonosaurus longiceps and Cynarioides gracilis.

It seems quite clear from the evidence so far produced that Galesaurus planiceps is a primitive cynodont lying between the gorgonopsians and such cynodonts as Thrinaxodon liorhinus, Gomphognathus mastacus, and Lycaenognathus platyceps. There is present in this series a progressive development of the prevomer from the gorgonopsians through Galesaurus planiceps to the more advanced cynodonts. This development consists primarily of two changes, the development of a medial ventral keel and an increase in length, both of which are associated with the development of the secondary palate.

The prevomer of Cyonosaurus longiceps and Cynarioides gracilis is without a keel. Galesaurus planiceps shows a ventral keel developed on the prevomer which serves as a medial nasal septum. In Thrinaxodon liorhinus, Gomphognathus mastacus, and Lycaenognathus platyceps the keel is extended further posteriorly.

An examination of the drawings of the animals in question indicates a progressive lengthening of the prevomer, in relation to the rest of the palate, from the two mentioned gorgonopsians through Galesaurus planiceps to the other cynodonts. There is also a progressive lengthening of the prevomer in relation to the length of the skull in the same series of animals. If the distance of the caudal end of the prevomer from the medial anterior end of the skull is compared with the length of the skull measured along the median line, on the palatal view, the following index could be determined:

$$\frac{\text{Distance of caudal end of prevomer from cranial end of palate} \times 100}{\text{Length of skull (palatal view)}} = \text{prevomer-skull index}$$

This value for the skulls studied is as follows:

Cynarioides gracilis	31.1	Thrinaxodon liorhinus	52.6
Cyonosaurus longiceps	39.8	Gomphognathus mastacus	57.4
Galesaurus planiceps	49.3	Lycaenognathus platyceps	62.7

These values may be questioned as indicative of phylogenetic trends, since they seem to be affected by the relative length of the snout to the cranium which often varies within the infra-ordinal groups. They are, however, suggestive of evolutionary developments.

Accompanying the development of the length and keel of the prevomer, there appears to be reduction of the parasphenoid. Broom's lateral view of the parasphenoid of Cynarioides gracilis shows a parasphenoid with a spur and a keel. These are seen to be reduced in the medial section of Galesaurus planiceps. The writer knows of no medial or lateral view of the parasphenoid of Thrinaxodon liorhinus, Gomphognathus mastacus, or Lycaenognathus platyceps from which to

judge the sagittal structure of their parasphenoids, but the palatal view of these forms shows the parasphenoid to be relatively shorter than in Cynarioides gracilis and Cyonosaurus longiceps but longer than in Galesaurus planiceps.

The development of the prevomer and the decrease of the parasphenoid in the cynodonts in comparison to the gorgonopsians seem to indicate:

1. That in the cynodonts there is a tendency to form the medial nasal septum from the prevomer and not from the parasphenoid.

2. The trend in the cynodont parasphenoid is opposite to that in the pelycosauria and gorgonopsians in which it tends to lengthen.

3. If the parasphenoid is homologous to the vomer, then the cynodonts which are known are off the line leading to the mammals, showing a definite trend away from the mammalian condition.

4. Broom is correct in concluding that Ictidosaurus is not a cynodont.

The last deduction follows from the developed parasphenoid of Ictidosaurus. Broom in his description of Ictidosaurus 'B,' states that, whereas the parasphenoid in the cynodonts is situated far back and the pterygoids unite in the middle line in front of it, in Ictidosaurus the parasphenoid is located in the middle of the skull and separates the pterygoids from each other.

Using the term 'vomer' in place of what has been called 'parasphenoid' in this study, Broom ('32 b) writes:

> The palate is partly preserved and of the greatest interest. In the cynodonts the vomer is far back and the pterygoids unite in the middle line in front of it. In this Ictidosaurian it is situated practically as in mammals, near the middle of the skull, and separates the pterygoids from each other. The back of the vomer doubtless rests on the basisphenoid and the front end probably passes forward as in mammals to support the secondary palate. Unfortunately the anterior part is lost but manifestly the vomer is quite a large bone, and quite clearly passes well forward considerably in advance of the pterygoids.

The cavity in the maxilla which is large enough to merit the name of a sinus may be homologous to the alveolar canal and the sinus maxillaris of the mammals. The sections of Cynarioides gracilis show that this animal lacked such a cavity.

The cranium

The bones which comprise the cranium of Galesaurus planiceps are the same as those that are found in the crania of gorgonopsians and of other cynodonts. The quadrate, quadratojugal, stapes, and interparietal, which are lacking in this specimen, are present in the Galesaurus planiceps described by Parrington ('34). Ornithorhynchus has a cranium which shows great changes from the condition of the cynodonts and the gorgonopsians. The opisthotic and the prootic are fused into the periotic. The interparietal and the quadratojugal are absent, and the quadrate has become the incus.

The size of the cranium is an item of interest. Galesaurus planiceps has a cranium which is comparatively larger than that of Thrinaxodon liorhinus, Gomphognathus mastacus, Lycaenognathus platyceps, Cyonosaurus longiceps, or Cynarioides gracilis. The increase in the relative size of this cranium over that of the gorgonopsians, a more primitive group, is to be expected, but its proportionate increase over cynodonts, which are from all other evidence more advanced, is, at first, surprising. An explanation, however, is found in the fact that the relative size of the head of a vertebrate decreases with an increase in the size of the body. Galesaurus planiceps is a small cynodont and hence should have a relatively large head.

The pineal opening is relatively larger both in the Galesaurus planiceps under discussion and Owen's type specimen than in the cynodont and the gorgonopsian forms mentioned above. This most probably is also due to the small size of Galesaurus planiceps, although some may regard it as a primitive characteristic.

There is a slight development of a sagittal crest in Galesaurus planiceps which seems to indicate a young stage of development, since Broom shows a clearly expressed crest in his diagram of a mature form.

The sagittal crest is lacking in the gorgonopsian forms. It is more pronounced in Thrinaxodon liorhinus, Gomphognathus mastacus, and Lycaenognathus platyceps than in the adult Galesaurus planiceps. This weak sagittal crest of Galesaurus planiceps is another primitive cynodont characteristic.

There is no evidence of sutures between the opisthotic and prootic in Galesaurus planiceps, Gomphognathus mastacus, Lycaenognathus platyceps, Cynarioides gracilis, and Cyonosaurus longiceps. This fusion is a mammalian tendency, but is expressed even in such primitive mammal-like reptiles as the pelycosaur, Dimetrodon.

Sections 22 and 23 show that the floor of the sella turcica does not reach the median line. This absence of bone may be due to erosion, since the right half of the floor of the sella is missing. But the medial edge of the preserved floor is even, which would argue against erosion and suggest that a canal was present in the floor of the sella. Since, however, the region is so damaged, and the writer knows of no other cynodont with a canal in this region, the latter interpretation must be regarded as very questionable.

Ear region. The difficult study of the comparative morphology of the ear will not be entered into in this investigation, but rather turned over to Dr. E. C. Olson, who has been engaged in this problem for some time. Only a few points will be mentioned.

The sections of Galesaurus planiceps skull show no traces of the endolymphatic duct which Watson found in Gomphognathus browni (Seeley), Broom (described by Watson, '13 b under the name of Diademodon entomophonus, Seeley).

The fenestra ovalis is relatively larger than Watson found in Gomphognathus browni. This large size seems to be a primitive cynodont characteristic.

G. G. Simpson ('33) describes the semicircular canals of the cynodonts as completely incased in bone. It is quite clear from the sections of the specimen studied in this paper that the semicircular canals are not completely incased in bone. A similar partial incasement in bone of these canals was found by Olson ('37) in Cyonosaurus longiceps. This incomplete incasement seems to be a primitive characteristic for Galesaurus planiceps.

The internal auditory meatus is relatively larger in Galesaurus planiceps than in Gomphognathus browni and smaller than in Cyonosaurus longiceps. This, too, would point to a primitive cynodont stage of evolution in Galesaurus planiceps. The subarcuate fossa for the flocculus indicates that the cerebellum filled its cavity. Watson ('13 b) found the same condition in Gomphognathus browni, as did Olson ('37) in Cyonosaurus longiceps. This is a mammalian trend.

The jaw

The jaw, although not completely preserved, presents a few interesting features.

The teeth were studied and discussed above.

There is a general reduction of the size of non-dentary bones of the jaw of Galesaurus planiceps over those of Cyonosaurus longiceps and Cynarioides gracilis. This reduction is carried much further in Gomphognathus mastacus and Lycaenognathus platyceps. Here, again, we have a primitive cynodont characteristic expressed in Galesaurus planiceps.

The splenial and articular of the specimen under consideration are relatively larger than in the two gorgonopsians and two cynodonts mentioned above. These enlargements seem to be specializations of Galesaurus planiceps. They add to the evidence indicating that Galesaurus planiceps if off the line leading to the mammals.

SUMMARY AND CONCLUSIONS

I. The skull of Galesaurus planiceps which has been sectioned is the skull of a young animal. Evidence for this is to

be found in the following features of the sectioned skull not found in Owen's type specimen, an adult animal:

1. Large size of the snout.
2. Large size of the nasal.
3. Postcanine formula of $\frac{PC\ 7}{PC\ 9}$. Owen's specimen and other skulls of Galesaurus planiceps have more postcanines.
4. Large size of the cranium.
5. Large size of the foramen pineale.
6. Slightly developed sagittal crest.

II. Galesaurus planiceps is a primitive cynodont. The evidence for this is the following:

1. Snout relatively larger than the average cynodont.
2. Lower set of teeth, when jaw is closed, lies within the upper.
3. Dental succession in caudal postcanines.
4. Distichial replacement of postcanines.
5. Foramen incisivum relatively large.
6. Secondary palate relatively short.
7. Premaxilla relatively small.
8. Facial exposure of septemaxilla.
9. Prevomer proportionately longer than in gorgonopsians and shorter than the average cynodont.
10. Keel of prevomer proportionately larger than that of gorgonopsians and smaller than that of other cynodonts.
11. Parasphenoid relatively smaller than that in the gorgonopsians and larger than that of the average cynodont.
12. Foramen pineale larger in comparison to the average cynodont (?).
13. Long quadrate process of the pterygoid.
14. Broad and low cranium.
15. Sagittal crest less developed than in average cynodont.
16. No trace of an endolymphatic duct.
17. Fenestra ovalis larger than in average cynodont.
18. Semicircular canals incompletely encased in bone.
19. Internal auditory meatus large.
20. Non-dentary jaw bones larger than in average cynodont.

III. Ictidosaurus is not a cynodont. Evidence for this is the following:

1. Reduction of the parasphenoid in the cynodonts. Broom considers the parasphenoid to be well developed in Ictidosaurus.

2. Prevomer forms nasal septum in cynodonts. Broom considers the nasal septum of Ictidosaurus to have developed from the parasphenoid.

IV. Galesaurus planiceps is off the direct line leading to the mammals:

1. A lacrimal larger than in the average cynodont, gorgonopsians, or in the primitive mammals.

2. Nasal septum developed from the prevomer. Broom considers the nasal septum of mammals to have developed from the parasphenoid.

3. Fusion of basisphenoid and basioccipital.

4. Splenial larger than in the gorgonopsians.

5. Articular larger than the articular of the gorgonopsians and the malleolus of the mammals.

6. Posterior forking of lacrimonasal duct.

V. Mammalian tendencies of the cynodonts which are not found in the gorgonopsians or are further developed than in the gorgonopsians:

1. Nasal expanded posteriorly as in the marsupials.

2. Lack of palatal teeth.

3. Presence of a sinus maxillaris (?).

4. Secondary palate.

5. Ectopterygoid smaller than in the gorgonopsians. The ectopterygoid is lacking in the mammals.

6. Subarcuate fossa well developed indicating that cerebellum filled its cavity.

7. Double occipital condyles.

VI. Characteristics which do not fall under the foregoing headings:

1. Nasal expanded anteriorly.

2. Large maxilla.

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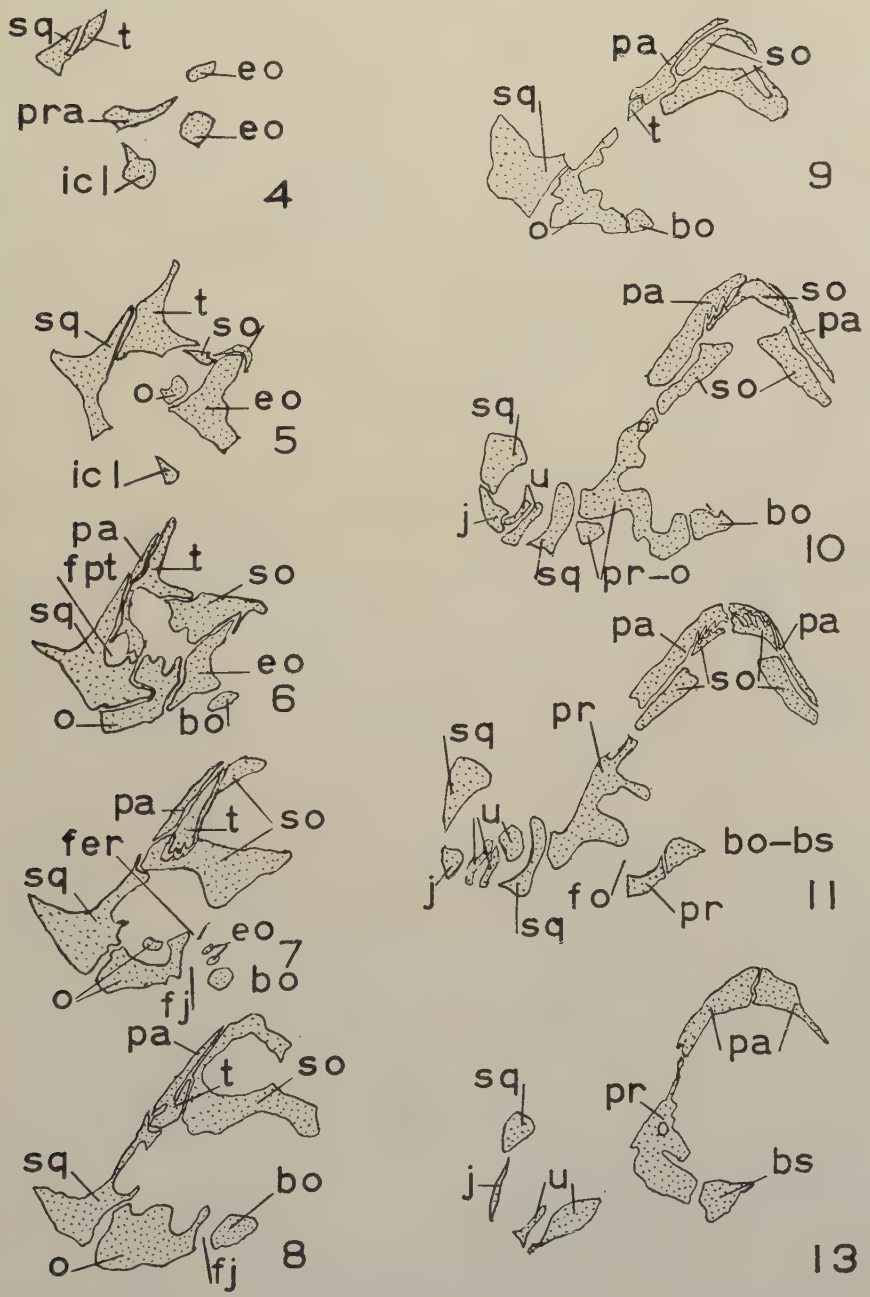
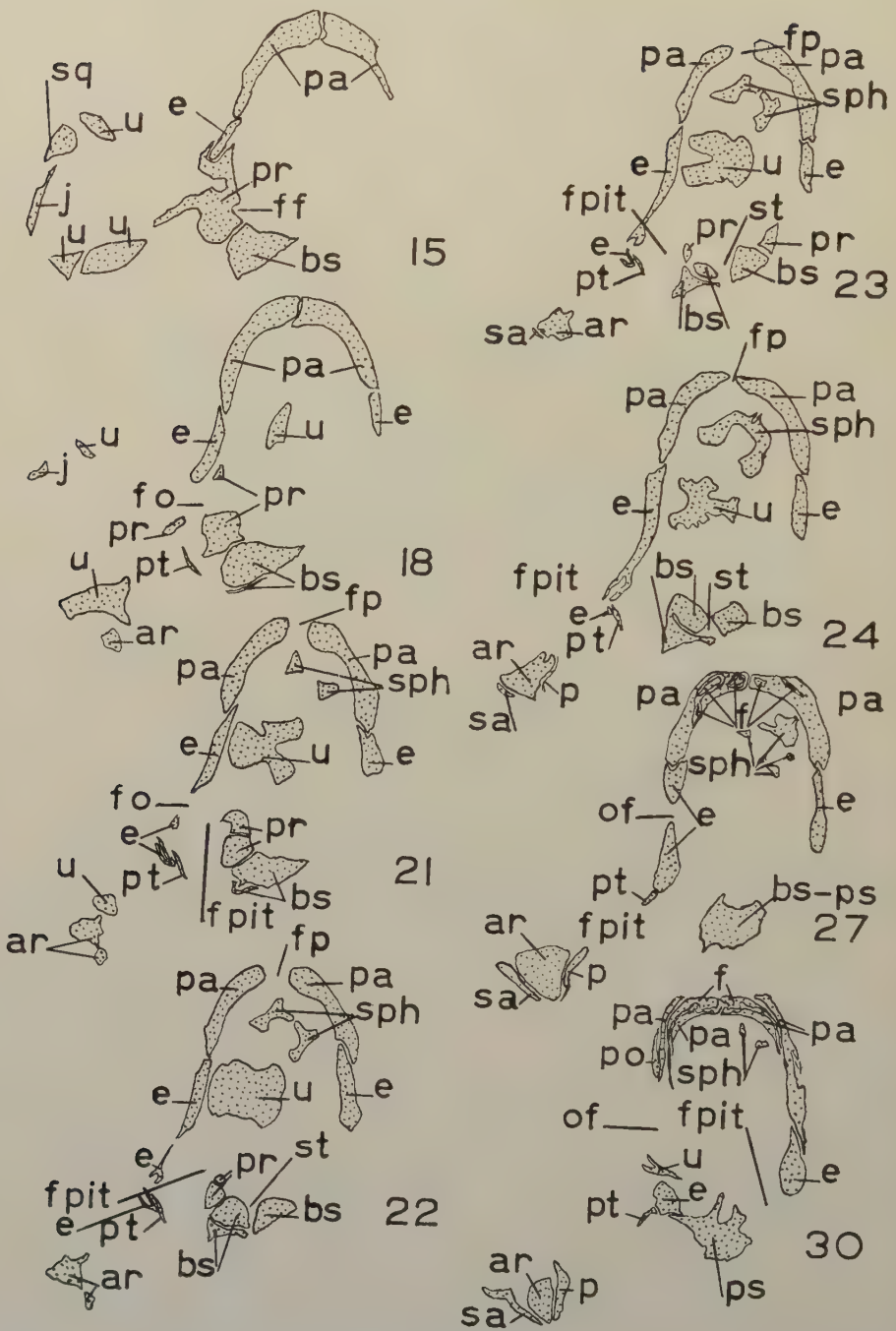
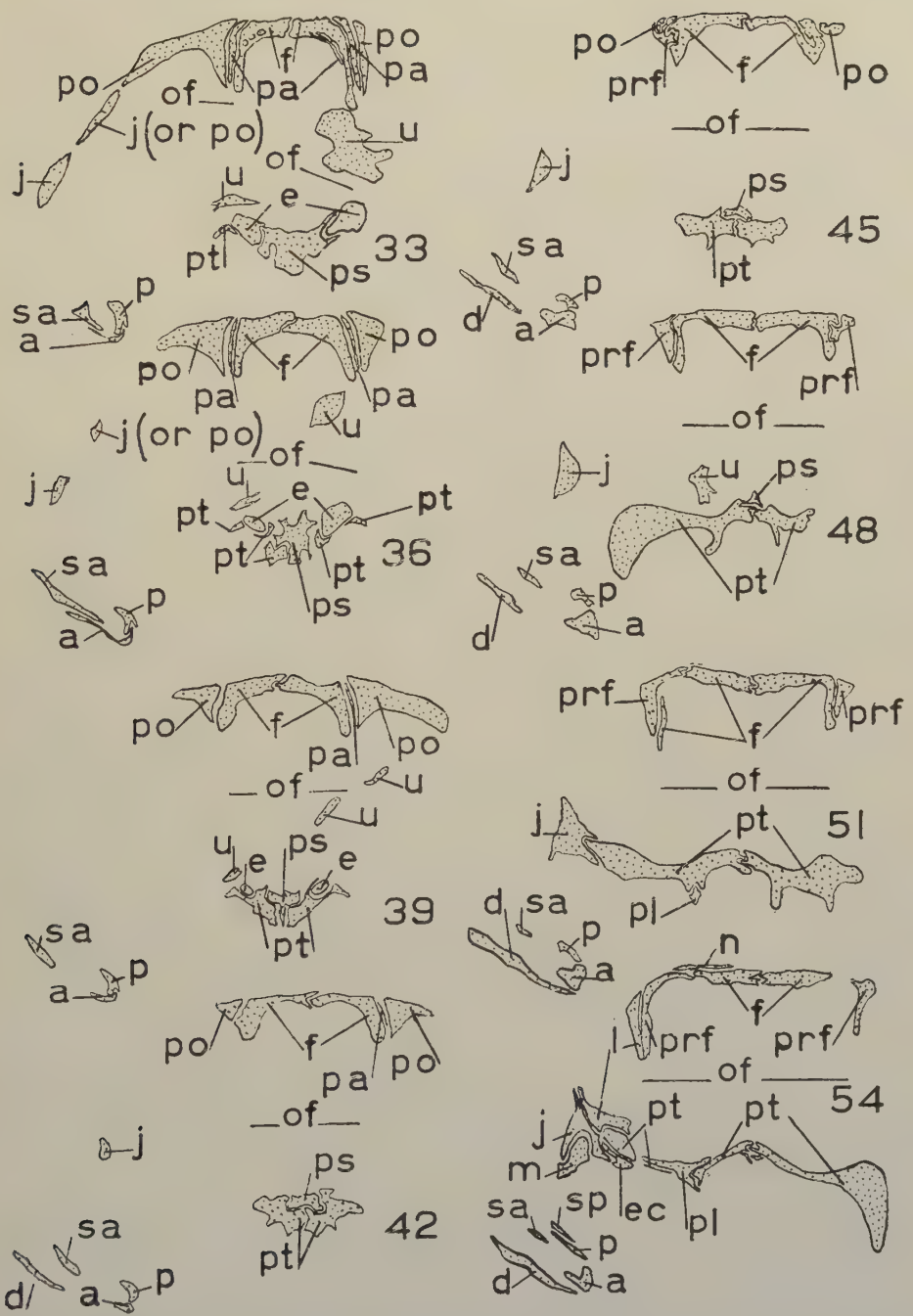
Skull of a young Galesaurus planiceps treated in this study. Ready to be embedded in plaster of Paris.



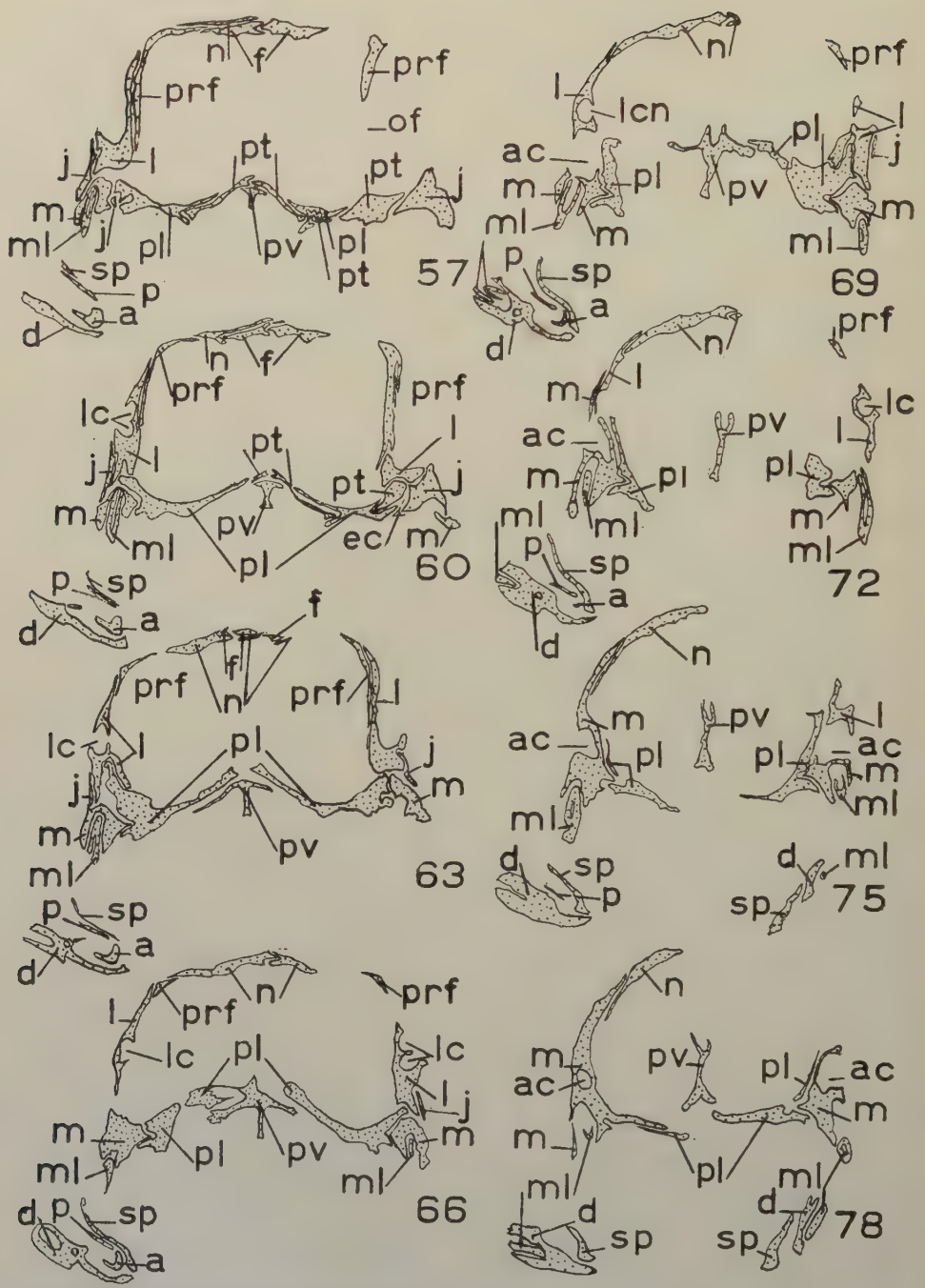
Sections 4, 5, 6, 7, 8, 9, 10, 11, and 13 of skull of a young Galesaurus planiceps.



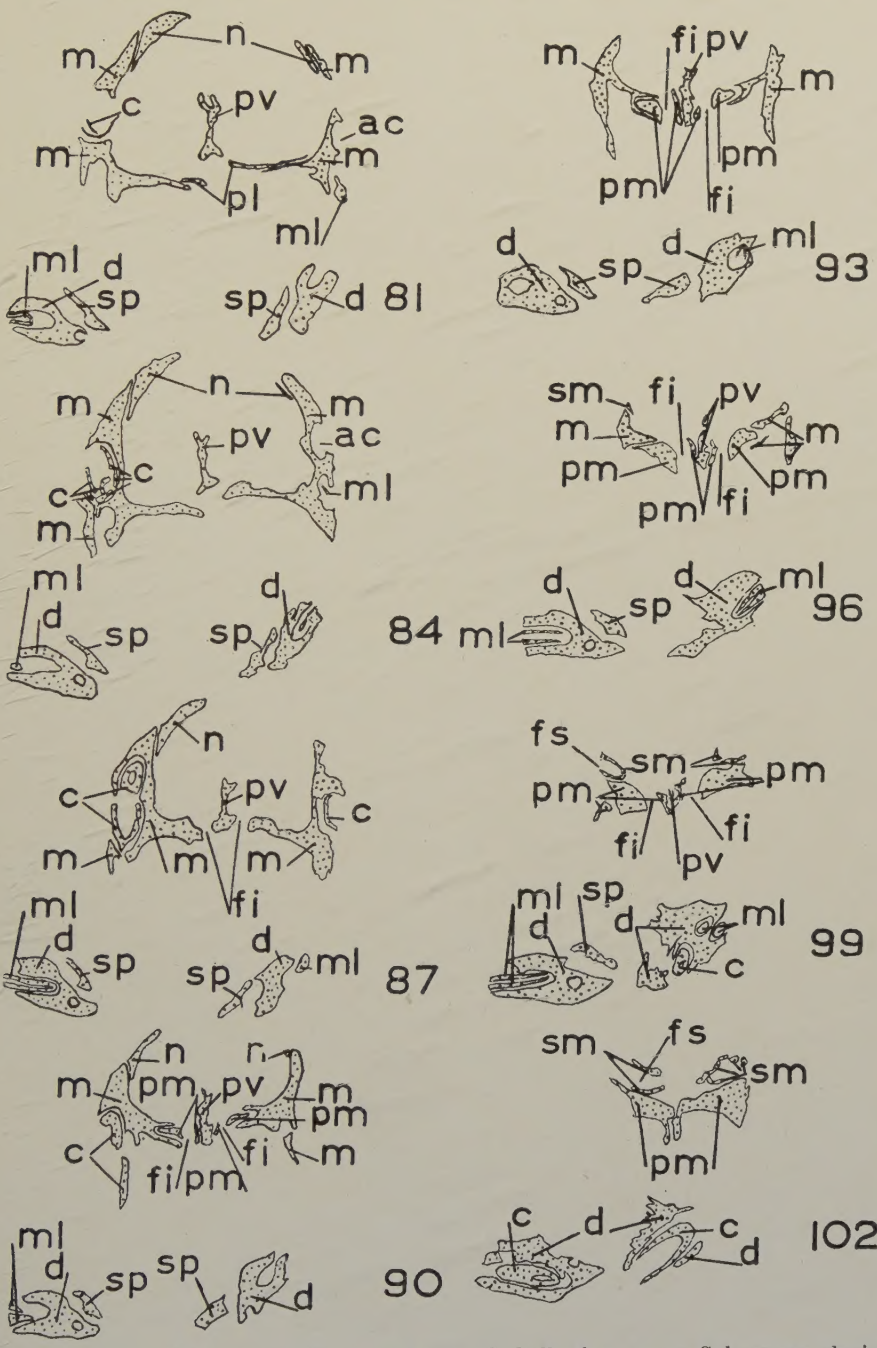
Sections 15, 18, 21, 22, 23, 24, 27, and 30 of skull of a young Galesaurus planiceps.



Sections 33, 36, 39, 42, 45, 48, 51, and 54 of skull of a young Galesaurus planiceps.



Sections 57, 60, 63, 66, 69, 72, 75, and 78 of skull of a young Galesaurus planiceps.



Sections 81, 84, 87, 90, 93, 96, 99, and 102 of skull of a young Galesaurus planiceps.